Scaling Metabolic Rate Fluctuations

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Running Head: Scaling Metabolic Rate Variability
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Abbreviations footnote: VO_2, metabolic rate (ml O2 /h) ; M, body size (g).

Abstract
Complex ecological and economic systems show fluctuations in macroscopic quantities such as exchange rates, size of companies or populations that follow non-gaussian tent-shaped probability distributions of growth rates, with power-law decay, which suggests that fluctuations in complex systems may be governed by universal mechanisms, independent of particular details and idiosyncrasies. We propose here that metabolic rate within individual organisms may be considered as an example of an emergent property of a complex system and test the hypothesis that the probability distribution of fluctuations in the metabolic rate of individuals has a 'universal' form regardless of body size or taxonomic affiliation. We examined data from 71 individuals belonging to 25 vertebrate species (birds, mammals and lizards). We report three main results. First, for all these individuals and species, the distribution of metabolic rate fluctuations follows a tent-shaped distribution with power-law decay. Second, the standard deviation of metabolic rate fluctuations decays as a power-law function of both average metabolic rate and body mass, with exponents -0.352 and –1/4 respectively. Finally, we find that the distributions of metabolic rate fluctuations for different organisms can all be rescaled to a single, parent distribution, supporting the existence of general principles underlying the structure and functioning of individual organisms.

Introduction

Living organisms have been described as the most complex system in the universe, emerging from the activity of an adaptive network of interacting components that allows energy, materials, and information to be acquired, stored, distributed and transformed (1, 2), and whose end result is the maintenance and reproduction of the network itself (3). A striking feature of complex systems is that they show regularities in the behavior of macroscopic variables, which emerge as the result of nonlinear interactions among multiple components and due to the competition of opposing control forces (4-6). These regularities commonly take the form of simple scaling relationships or power-laws (7, 8). A macroscopic variable that shows scaling relationships is metabolic rate, the rate at which an animal consumes oxygen (VO_2), which scales with body mass (M) such that $VO_2 \propto M^{\alpha}$ with $\alpha<1$.

For over a century, biologists have documented and tried to explain both the value of α, and the effects ecological factors have on it (1, 9-17). Most of these studies focus on average values of VO_2 and M, and do not consider the temporal variability in individual energy use. However, physiological variables such as cardiac and breathing dynamics display complex rhythms, which often show changes both with disease and aging (17-20). In this context, the study of fluctuations in VO_2 can shed light on the determinants of metabolic scaling, and provide a way to test competing models and explanations. Indeed, work on complex systems has shown that study of the scaling properties of fluctuations in macroscopic quantities can provide insights on the processes responsible for the macroscopic behavior, even in the absence of detailed mechanistic descriptions of the functioning of the system (4-6). Most comparative analyses of VO_2 variability study circadian rhythms (21-24), and do not examine high frequency variation. In this contribution, we argue that the study of high frequency fluctuations in VO_2 across different species may provide insights on the processes determining its dynamics and their interaction with body size and physiology.

In general terms, the rates of whole body VO_2 displayed by animals represent the interaction between a supply component, represented by the network that supplies metabolic substrates, removes waste products and regulates activity and a demand component, represented by the sum of cellular respiration rates in various metabolically active organs within the whole organism. Although the relative importance of supply and demand components in accounting for metabolic rate, and in particular for the value of the scaling exponent α, is still debated (1, 14, 16, 17), it is accepted that in order to maintain homeostasis, living organisms must allocate their available resources to meet the demands of different organs and their component tissues. This has for long been recognized by physiological ecologists in the context of allocation to generic functions such as growth, reproduction and maintenance (25, 26). In this regard, the allocation of limited resources to varying functions implies the existence of a complex web of competing forces, which together drive the resultant metabolism. Furthermore, some of

the processes involved in the supply of oxygen and its consumption at cellular level are usually driven by competing forces, such as the case of respiratory and cardiac systems, which respond to parasympathetic versus sympathetic stimuli from the autonomic control system (27, 28). These two characteristics, the emergence of a macroscopic phenomenon (in this case whole body VO_2) from microscopic interactions with a large number of degrees of freedom and the competition of opposing control forces, are hallmarks of complex systems such as those studied in statistical physics and economy(4, 6).

In recent years, Stanley and co-workers (29-31) have studied fluctuations in diverse complex systems such as business firms, countries, universities and bird assemblages, and have shown that, despite the many striking differences setting them apart, they all show non-gaussian tent-shaped distributions of growth rates with power-law decay. This has led to the proposition that the fluctuations of complex systems are governed by universal mechanisms, independent of particular details and idiosyncrasies (4, 5, 29, 31). If this is so, this hypothesis should hold true in other complex systems, and thus we should expect the statistical properties of fluctuations in VO_2 of individual animals to follow these universal laws. In this context, we aim to test the working hypothesis that the distributions of VO_2 fluctuations of individual organisms in different species follow a tent shaped distribution. Further, since biological rates, such as breathing or heart rate, scale as M raised to the –1/4 power (11, 32, 33) it can be expected that the magnitude of relative fluctuations in VO_2 should decrease with increasing body mass following a –1/4 power. This implies that much of the variability in VO_2 fluctuations can be accounted for by rescaling the original distribution by its observed standard deviation. We thus expect that all distributions, regardless of species, sex and size will collapse to an universal distribution of fluctuations under rescaling.

Results

We studied VO_2 time series for 71 individuals belonging to 25 species of small terrestrial vertebrates (10 bird species, 12 small mammals and 3 lizards) (see Table 1 of the Supplementary Information). We found that, for all individuals studied, the conditional probability density of VO_2 fluctuations $p(r|v)$ has a simple 'tent' shape, although with different widths. Given that individuals of the same species did not differ greatly in their body sizes, we pooled the information from conspecific individuals, and then compared the distributions of fluctuations between different species (Table 2 of the Supplementary Information shows results for individual organisms). Figure 1 shows the results for a subset of the species we studied. This tent-shaped distribution corresponds to the double exponential or Laplace distribution (29, 34)

$$p(r|v) = \frac{1}{\sqrt{2}\sigma_r(v)} \exp\left(\frac{\sqrt{2}|r - \langle r \rangle|}{\sigma_r(v)} \right) \qquad (1)$$

where $\langle r \rangle$ and $\sigma_r(v)$ correspond to the mean and standard deviation of VO_2 growth rates respectively. A likelihood ratio test statistic (34, 35) showed this fit to be statistically

significant for all the species studied, and different from a gaussian distribution, which is to be expected if system components vary independently of each other (see Table 3 of the Supplementary Information for tests results at the individual and species level). In agreement with this result the variation in the width of the distribution of the VO_2 growth rates, measured by its standard deviation $\sigma_r(v)$ is as a function of $\langle VO_2 \rangle$, the average rate of oxygen consumption. Figure 2A shows that, despite residual variation in the data, $\sigma_r(v)$ scales as a power-law

$$\sigma_r(v) \propto \langle VO_2 \rangle^{\beta} \qquad (2)$$

with an exponent $\beta = -0.352 \pm 0.072$ (OLS regression estimate ± 1SE, 95% confidence interval: -0.208 to -0.496). On the other hand, $\sigma_r(v)$ scales with body mass as

$$\sigma_r(v) \propto M^{\gamma} \qquad (3)$$

with $\gamma = -0.241 \pm 0.103$ (OLS regression estimate ± 1SE, 95% confidence interval: -0.035 to -0.447), which does not differ from the expected -1/4 exponent.

The fact that all these species show the same scale invariant probability distribution of VO_2 fluctuations, regardless of the differences in their phylogeny, physiology and body size, suggests that they are expressions of a more general phenomenon. If this is indeed the case, we expect these distributions to show data collapse under adequate rescaling (29, 31). Figure 2B shows that when we plot the scaled probability density function $p_{scal} = \sqrt{2}\sigma_r(v)p(r|v)$ against the scaled growth rate $r_{scal} = \frac{\sqrt{2}\left[r - \langle r(v) \rangle\right]}{\sigma_r(v)}$, the observed distributions for all the species do indeed collapse, with data from all the species converging onto a single scaling curve $p_{scal} = \exp(-|r_{scal}|)$.

Discussion

Our results show that the distribution of metabolic rate fluctuations follows a tent-shaped distribution rather than the normal distribution expected from the null model of a random multiplicative process. This is not so surprising if one considers that such a null model implies that $\log(VO_2)$ follows a random walk, and hence is not regulated. However, metabolic rate is under homeostatic regulation, and must show dynamic feedback structure. A simple dynamical model showing such a feedback is the biased random walk,

$$\frac{VO_2(t+\Delta t)}{VO_2(t)} = \begin{cases} k(1+\varepsilon_t) & \text{for } VO_2 < VO_2^* \\ \frac{1}{k}(1+\varepsilon_t) & \text{for } VO_2 > VO_2^* \end{cases} \qquad (4)$$

where k is a constant larger than one measuring the strength of the feedback input biasing the random walk towards a preferred value, and ε_t are uncorrelated gaussian random numbers with zero mean and variance $\sigma_\varepsilon^2 << 1$. For this well-studied problem, r is distributed according to equation (1) (29). Extensions of this model, that include more than one scale of regulation, have been shown to generate complex

dynamics similar to those observed in other physiological variables (36). Thus, the non-normality of VO_2 fluctuations provides evidence of homeostatic regulation or feedbacks acting on VO_2.

It has been argued the tent-shaped distributions of growth rates in complex systems may emerge if the units composing the system evolve according to a random multiplicative growth process (e.g. a mixture of lognormal distributions with different variances) (37, 38). However, for this explanation to hold in our system, it would be required that the amount of oxygen consumed by the units composing the system (i.e. cells, tissues or organs) would be independent, with similar mean and different variances. Notwithstanding that the assumption of independent energy use is likely a strong one (see discussion below), considering that energy is usually limited and its allocation to different functions (growth, storage and reproduction) and trade-offs has fitness consequences (39) we cannot at present provide a definitive test of this explanation as this would require the availability of measurements of metabolic rate dynamics at the level of cells, tissues and organs within living organisms. Further research on the statistical patterns of VO_2 dynamics within individuals and across different species are needed to gain a better understanding of the nature of the homeostatic processes acting on this emergent attribute of individual organisms.

Our second result is the power-law decay of the width of the distribution $p(r|v)$ as a function of both average metabolic rate and body size. The simplest model to explain the dependence of $\sigma_r(v)$ on $\langle VO_2 \rangle$ would be to assume that an organism is made up of n equally sized cells of mass m_c, each consuming oxygen at independent rates. The central limit theorem predicts $\sigma_r(v)$ decays as $n^{-1/2}$ or equivalently under this general assumption, as $M^{-1/2}$ (37, 40). If $\langle VO_2 \rangle$ is assumed to be proportional to n, we would also expect that $\sigma_r(v) \propto \langle VO_2 \rangle^{-1/2}$. However, the decay in VO_2 fluctuations is much slower, and both β and γ are larger that -1/2 ($\beta = -0.352 \pm 0.072$ s.e. and $\gamma = -0.241 \pm 0.103$ s.e.). This suggests that cellular oxygen consumption rates are not independent within an organism, further reinforcing the existence of physiological feedbacks, which do not fully synchronize all cells. On the other hand, if all cells were strongly correlated, then it should not matter what size the organism is, and we should find that $\beta=\gamma=0$. Interestingly, it can be shown that the scaling of VO_2 fluctuations is related to the more widely studied allometric scaling of VO_2 by the following expression $\gamma=\alpha \cdot \beta$. This predicts a value of $\gamma=-0.27 \pm 0.14$ (s.e.), which does not differ from the observed -1/4 value. Future research may be directed to examining whether dynamical extensions of existing explanations of the allometry of VO_2, either the supply limitation (1) or the multiple control model (16) can predict statistical patterns in VO_2 variability.

In closing, we want to emphasize that individual organisms are complex systems, whose study could provide the basis for a deeper understanding of complex ecological and economic systems, which unlike individuals, do not allow for controlled experimentation. The universality of tent-shaped distributions for VO_2 fluctuations across individuals belonging to species that differ in many regards, including the details

of their respiratory system, their thermal physiology, and body size supports the claim that complex biological systems show power-law dependence in emergent quantities, the same as do other physical and economic systems. Reconciling or resolving the apparent contradiction between such universal patterns and the observed diversity of form and function in animal taxa is an emerging challenge for scientists working at the interface between evolutionary biology, physiology and complex systems sciences.

Materials and Methods

Determination of Individual Metabolic Rate: To study the scaling properties of metabolic rate fluctuations, we recorded VO_2 time series for individual organisms at rest during observation periods averaging 1 hour. To determine VO_2 we transferred individuals of different species of small terrestrial vertebrates (mammals, birds and lizards) to the laboratory and housed them individually. VO_2 was determined according to the following protocol for measurements collected over a three-hour period during mid-morning. Birds were measured in dark metabolic chambers. Oxygen consumption was measured in a computerized (Datacan V™) open-flow respirometry system (Sable Systems, Henderson, Nevada). The metabolic chamber received dried air at a rate ranging form 500 to 1000 ml/min from mass flow-controllers (Sierra Instruments ™, Monterey, California), which ensured adequate mixing in the chamber. In all cases the metabolic chambers allowed the animals a limited amount of movement. It is important to note that, while these movements could potentially increase the observed metabolic rate, all measurements were done in the rest phase of the circadian cycle of these species. Air passed through CO_2 and H_2O absorbent granules of Baralyme™ and Drierite™ respectively before and after passing through the chamber and was monitored every 5 s by an Applied Electrochemistry O2-analyzer, model S-3A/I (Ametek™, Pittsburgh, Pennsylvania).

Birds and mammals were fed ad libitum with bird seed and rabbit food pellets respectively, while lizards were fed mealworms (*Tenebrio molitor*). Water was also provided ad libitum. Ambient temperature (Ta) and photoperiod were held constant at 20 ± 2ºC and 12L: 12D. Animals were held for one and two days prior to VO_2 measurements and then fasted for 6-12 h. before placement in metabolic chambers, at Ta within the thermoneutral zone of each endothermic species ((41-43). Standard metabolic rates of lizards were measured at Ta=30°C. Individual body size was measured using a digital balance at the beginning and at the end of each experiment. All experiments with animal subjects were conducted according to current Chilean law for ethical manipulation of laboratory animals and under permits issued from Servicio Agrícola y Ganadero.

Data Processing and Analysis: In order to study the statistical properties of fluctuations in VO_2, we examine its variation within a single organism during a given period of time (averaging 1 hour of observation). The fluctuations of a variable may be described by

many quantitative descriptors, such as their periodicity, amplitude, and frequency spectrum (44). However, as a first approximation, we choose as our measure of variability the growth rate of VO_2 in logarithmic scale, and so we define $r \equiv \log\left[\frac{VO_2(t+\tau)}{VO_2(t)}\right]$ where $VO_2\ (t)$ and $VO_2\ (t+\tau)$ are the metabolic rates observed for a given individual in time intervals t and t+τ, respectively. This measure has the advantage that it removes the effect of any trends, and hence is not affected by changes in the average value of the variable (6). We also define $\nu = \log\left[\langle VO_2 \rangle\right]$, the logarithm of the average metabolic rate observed over the study period. We then calculate the conditional probability density distribution, p(r |ν), of growth rates r for each species with a given ν.

The simplest model for the fluctuations in VO_2 is one that assumes that it fluctuates independently of organism size, and that successive fluctuations are uncorrelated in time. These assumptions can be formalized in a simple random multiplicative process, which predicts that VO_2 values should be log-normally distributed (28). A direct consequence of this is that p(r |ν) follows a Gaussian distribution, which would show in our graphs as a parabola. We take this as our null hypothesis for the fluctuations of VO_2. On the other hand, studies on other complex systems have shown that p(r |ν) can be described by a Laplace distribution (eqn. 1) (28-30, 34, 37) Therefore, for each of the species studied, we tested the hypothesis that the conditional probability density p(r|ν) fits either a Laplace or a Gaussian distribution using a likelihood ratio test statistic (see refs 34 and 35 for details).

If the conditional probability density functions of different individuals or species follow the same functional form, one would expect that under a non-trivial scale transformation that all of these distributions should converge or collapse into a single statistical distribution. By 'scaling', we mean applying the same function of observed parameters to the distributions. If the scaling holds, then, data for a wide range of parameter values (in this case values of ν and $\sigma_r(\nu)$) are said to 'collapse' upon a single curve. One key parameter in the rescaling procedure is the width of the conditional distribution p(r|ν). It can be expected that the magnitude of fluctuations should decrease with increasing body mass following a –1/4 power (11, 45, 46), so that VO_2 in smaller individuals should fluctuate more in than large ones. The magnitude of the variability or fluctuations in a variable can be measured by examining the standard deviation of growth rates, $\sigma_r(\nu)$. Thus, we also examined the possible effects of average metabolic rate and body size on the magnitude of VO_2 fluctuations as measured by the value of $\sigma_r(\nu)$ by plotting the scaling relationship between these two variables. Given the low measurement error rate in both body size (47) and VO_2 we estimated the scaling exponent using OLS regression.

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Figure Legends

Figure 1: Fluctuations of metabolic rate in terrestrial vertebrates. (A). Conditional probability density function $p(r|\nu)$ of the growth rates r in three lizard species. (B). Conditional probability density function $p(r|\nu)$ of the growth rates r in five bird species. (C). Conditional probability density function $p(r|\nu)$ of the growth rates r in four small mammal species. For all three figures, the solid lines are fits to equation (1) using the mean $\langle r \rangle$ and standard deviation $\sigma_r(\nu)$ calculated for the data from each species.

Figure 2: Scaling and universality of metabolic rate fluctuations. (A). Filled circles show average standard deviation $\sigma_r(\nu)$ of observed metabolic rate fluctuations as a function of average metabolic rate $\langle VO_2 \rangle$. The solid line shows a least squares regression fit to the log transformed data, with slope β=0.325±0.07. Error bars show one standard error. Also shown in open circles are the data observed for each species. (B). Scaled probability density function $p_{scal} = \sqrt{2}\sigma_r(\nu)p(r|\nu)$ plotted against the scaled growth rate $r_{scal} = \dfrac{\sqrt{2}\left[r - \langle r(\nu) \rangle\right]}{\sigma_r(\nu)}$ for all the species shown in Figure 1. Note that the scaled data collapse onto the single scaling curve $p_{scal} = \exp(-|r_{scal}|)$.

Figure 1

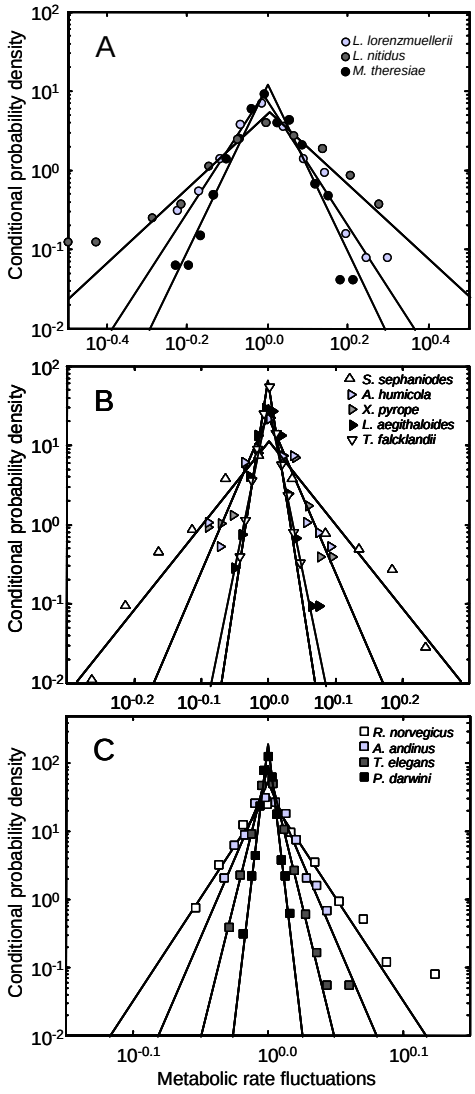
A
L. lorenzmuellerii
L. nitidus
M. theresiae
B
S. sephaniodes
A. humicola
X. pyrope
L. aegithaloides
T. falcklandii
C
R. norvegicus
A. andinus
T. elegans
P. darwini
Conditional probability density
Metabolic rate fluctuations

Figure 2

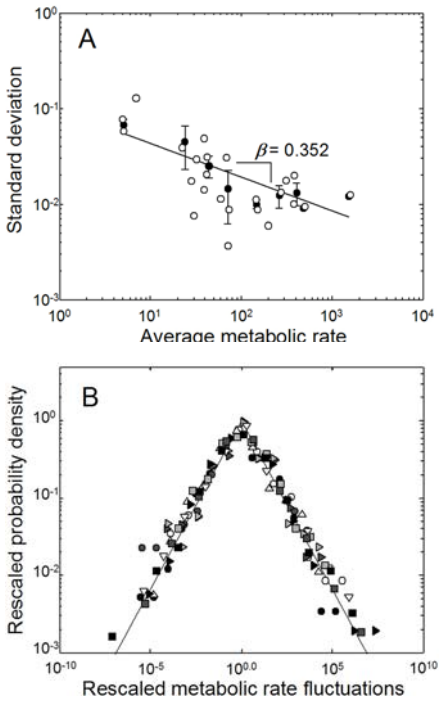
A
Standard deviation
β= 0.352
Average metabolic rate
B
Rescaled probability density
Rescaled metabolic rate fluctuations

Table S1: List of species studied.

Class	Order	Family	Species
Aves	Apodiformes	Trochilidae	*Patagona gigas*
		Trochilidae	*Oreotrochilus estella*
		Trochilidae	*Rhodopis vesper*
		Trochilidae	*Sephanoides galeritus*
	Passeriformes	Furnariidae	*Lepstastenura aegithaloides*
		Furnariidae	*Asthenes humicola*
		Muscicapidae	*Turdus falcklandii*
		Phytotomidae	*Phytotoma rara*
		Tyrannidae	*Elaenia albiceps*
		Tyrannidae	*Xolmis pyrope*
Mammalia	Lagomorpha	Leporidae	*Oryctolagus cuniculus*
	Marsupialia	Dideplhidae	*Thylamis elegans*
	Rodentia	Abrocomidae	*Abrocoma benetti*
		Caviidae	*Microcavia niata*
		Cricetidae	*Phyllotis Darwinii*
		Cricetidae	*Abrothix andinus*
		Ctenomydae	*Ctenomys sp.*
		Muridae	*Rattus norvegicus*
		Octodontidae	*Octodon degus*
		Octodontidae	*Octodontomys gliroides*
		Octodontidae	*Octodon lunatus*
		Octodontidae	*Spalacopus cyanus*
Reptilia	Sauria	Tropiduridae	*Microlophus teresoides*
		Tropiduridae	*Liolaemus lorenzmuellerii*
		Tropiduridae	*Liolaemus nitidus*

Table S2: Results of maximum likelihood ratio test of the growth rate distribution for individual organisms studied. The table indicates the species studied, body size, mean VO_2 ($\langle VO_2 \rangle$), average VO_2 growth rate($\langle r \rangle$), the number of observations (data points) analyzed per individual, as well as the probability of the likelihood ratio test (P).

Species	Body Size (g)	$\langle VO_2 \rangle$ (mol O2/gh)	$\langle r \rangle$	Number of observations	P
Patagona gigas	24.62	79.0	-3.84E-05	819	1.53E-75
Patagona gigas	20.8	68.5	3.87E-05	368	6.81E-12
Oreotrochilus estella	6.72	33.7	-2.17E-04	222	1.50E-03
Oreotrochilus estella	8.7	42.3	-2.88E-04	1365	1.85E-28
Oreotrochilus estella	7.1	42.7	-4.27E-04	1981	1.47E-59
Rhodopis vesper	4.67	28.4	-9.41E-06	1765	3.89E-105
Rhodopis vesper	5.78	32.8	-2.07E-04	367	1.57E-02
Rhodopis vesper	5	40.0	-4.37E-05	1876	1.48E-05
Rhodopis vesper	4.8	27.9	-5.47E-05	2096	5.85E-208
Sephanoides galeritus	5.25	21.9	-1.86E-03	120	2.07E-04
Sephanoides galeritus	5.75	22.2	-6.92E-04	185	9.41E-05
Sephanoides galeritus	5.18	37.3	-1.96E-03	89	2.90E-03
Lepstastenura aegithaloides	8.1	25.8	-1.98E-04	605	2.80E-03
Lepstastenura aegithaloides	8	38.9	1.45E-03	357	3.91E-06
Asthenes humicola	18.5	42.6	9.77E-04	216	3.71E-13
Turdus falcklandii	71.7	121.7	2.08E-05	920	1.68E-105
Turdus falcklandii	61	125.9	-1.24E-04	945	1.88E-68
Turdus falcklandii	68	139.0	-1.04E-05	746	2.20E-03
Turdus falcklandii	68.8	140.9	-5.00E-05	437	6.42E-48
Turdus falcklandii	72	169.0	-3.39E-04	500	1.55E-19
Phytotoma rara	43	174.7	8.32E-05	2048	0.00E+00
Phytotoma rara	41.6	206.2	3.84E-05	2048	5.39E-24
Phytotoma rara	45.3	133.1	3.25E-04	2048	1.12E-122
Phytotoma rara	41.3	190.8	1.52E-05	2048	6.75E-76
Phytotoma rara	38.7	174.0	-1.77E-05	2048	4.44E-202
Elaenia albiceps	13.3	23.2	-1.34E-04	504	4.79E-04
Elaenia albiceps	14	45.8	-7.06E-04	282	2.18E-02
Elaenia albiceps	13.1	49.3	-2.73E-04	260	4.19E-06
Xolmis pyrope	29.41	74.9	-6.53E-05	432	6.50E-28
Oryctolagus cuniculus	2300	1481.1	-3.02E-05	861	5.16E-33
Oryctolagus cuniculus	3100	1573.6	-1.37E-04	1267	3.78E-69
Thylamis elegans	36.1	25.6	-3.95E-04	247	6.40E-02
Thylamis elegans	28.4	28.1	-4.13E-04	479	1.38E-06
Thylamis elegans	32.3	37.1	-1.47E-04	1540	1.35E-98

Table S2 cont.:

Species	Body Size (g)	<VO_2> (mol O2/gh)	<*r*>	Number of observations	P
Abrocoma benetti	284	239.3	1.31E-04	993	2.86E-198
Abrocoma benetti	230.6	370.6	-9.59E-05	276	1.91E-30
Abrocoma benetti	241.5	324.0	3.57E-05	1060	4.66E-106
Abrocoma benetti	196.1	252.1	-3.95E-05	1773	1.70E-20
Microcavia niata	246.6	701.9	-6.44E-05	1116	1.82E-18
Microcavia niata	270.5	524.2	-1.86E-05	1111	3.29E-40
Microcavia niata	265.3	407.7	2.44E-04	359	5.94E-42
Microcavia niata	285.3	522.4	3.06E-05	1304	1.37E-70
Phyllotis Darwinii	67.7	85.1	-1.31E-04	1527	2.10E-61
Phyllotis Darwinii	60.1	61.8	-1.46E-03	116	1.56E-07
Phyllotis Darwinii	66.1	68.8	-2.38E-04	724	1.26E-10
Abrothix andinus	15.7	34.3	-9.62E-04	446	3.24E-05
Abrothix andinus	17	25.9	-2.63E-06	475	8.40E-03
Abrothix andinus	17.7	25.1	-1.16E-04	191	8.80E-03
Ctenomys sp.	274.7	330.8	-4.10E-04	871	8.57E-65
Ctenomys sp.	194.5	246.3	3.83E-05	651	4.62E-31
Ctenomys sp.	197.4	323.6	7.75E-05	712	1.64E-79
Ctenomys sp.	210.8	353.6	5.79E-05	910	9.56E-56
Ctenomys sp.	214.4	294.3	3.71E-05	731	2.25E-126
Rattus norvegicus	500	443.3	-3.16E-05	1317	8.88E-46
Rattus norvegicus	500	374.5	1.15E-05	1238	1.89E-71
Octodon degus	201.8	168.4	-8.31E-03	228	1.09E-02
Octodon degus	149.7	181.8	-8.70E-05	85	2.20E-03
Octodon degus	250.9	244.2	-1.61E-04	274	5.92E-17
Octodontomys gliroides	125.7	450.7	-3.04E-04	948	5.40E-113
Octodontomys gliroides	157.7	534.5	-3.74E-04	427	3.41E-23
Octodontomys gliroides	122	480.7	-1.21E-04	889	1.24E-45
Octodon lunatus	229.9	364.0	-1.11E-04	1570	2.14E-102
Spalacopus cyanus	108.1	81.8	-5.56E-04	196	5.30E-03
Spalacopus cyanus	113	37.9	6.52E-02	392	3.17E-14
Microlophus teresoides	24.5	5.1	-6.45E-05	1491	7.86E-28
Liolaemus lorenzmuellerii	25	6.2	-8.60E-03	75	3.56E-32
Liolaemus lorenzmuellerii	28.3	2.9	-1.29E-02	67	2.51E-08
Liolaemus lorenzmuellerii	27.6	6.3	-1.29E-02	49	4.75E-15
Liolaemus lorenzmuellerii	33.4	4.6	-7.07E-03	55	5.82E-13
Liolaemus nitidus	28.3	9.8	4.71E-03	54	3.15E-09
Liolaemus nitidus	27.6	4.4	5.61E-03	61	2.28E-02

Table S3: Results of maximum likelihood ratio test of the growth rate distribution at the species level. The table indicates the species studied, mean body size, mean VO2, (<VO_2>), average VO_2 growth rate(<*r*>), the number of observations (data points) analyzed per species as well as the probability of the likelihood ratio test.

Species	Number of individuals	Mean Body Size (g)	Mean VO_2 (mol O2/gh)	Mean r	Number of observations	P
Patagona gigas	2	22.7	73.8	-0.0002	1187	6.27E-77
Oreotrochilus estella	3	7.5	41. 5	-0.0013	552	1.60E-04
Rhodopis vesper	4	5.8	32.1	-0.0003	1220	1.10E-94
Sephanoides galeritus	3	5.8	22.2	-0.0013	394	2.22E-14
Lepstastenura aegithaloides	2	8.0	38. 9	0.0004	962	9.79E-05
Asthenes humicola	1	18.5	42. 6	0.0010	216	3.71E-13
Turdus falcklandii	5	68.4	145.3	-0.0001	3548	7.11E-262
Phytotoma rara	5	41.7	152.0	0.0000	8192	0.00E+00
Elaenia albiceps	3	13.8	38.5	-0.0003	1046	4.82E-30
Xolmis pyrope	1	29.4	69.7	0.0005	432	6.50E-28
Oryctolagus cuniculus	2	2700.0	1527. 4	-0.0001	3609	1.14E-185
Thylamis elegans	3	32.3	30.3	-0.0002	2266	5.60E-90
Abrocoma benetti	4	236.1	275.6	1.7378E-05	4102	1.28E-280
Microcavia niata	4	266.9	483.8	0.0000	846	7.76E-86
Phyllotis Darwinii	3	64.6	71.9	-0.0004	1027	2.70E-20
Abrothix andinus	3	236.1	275.6	-0.0003	574	2.70E-03
Ctenomys sp.	5	218.4	309.7	-0.0001	3875	0.00E+00
Rattus norvegicus	2	500.0	383.3	0.0000	1438	1.12E-89
Octodon degus	3	200.8	198.2	0.0001	587	2.41E-43
Octodontomys gliroides	3	135.1	488.6	-0.0002	2246	8.32E-167
Octodon lunatus	1	229.9	375.6	-0.0001	1570	2.14E-102
Spalacopus cyanus	2	110.6	59.9	-0.0005	588	4.58E-79
Microlophus teresoides	1	24.5	5.072	-0.0001	1491	7.86E-28
Liolaemus lorenzmuellerii	4	17.2	4.985	-0.0103	246	6.82E-06
Liolaemus nitidus	2	28.6	6.927	0.0052	115	3.57E-04